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Zoology: Molluscs All Beneath the Sun, One Shell, Two Shells, More, or None

Sigwart, J. D. (2017). Zoology: Molluscs All Beneath the Sun, One Shell, Two Shells, More, or None. *Current Biology*, 27(14), R708-R710. <https://doi.org/10.1016/j.cub.2017.05.075>

Published in:
Current Biology

Document Version:
Peer reviewed version

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This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No H2020-MSCA-IF-2014-655661.

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DISPATCH

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One great remaining problem in evolutionary biology is to understand which common ancestor could have given rise to descendants as different as giant squid and microscopic pea clams. Two new papers provide important insights to molluscan body plan disparity.

Julia D. Sigwart^{1,2}

Molluscs are both familiar and mysterious. Gastropods (snails and slugs), bivalves (clams and oysters) and cephalopods (octopus and squid) are of global economic importance (Figure 1). The other five taxonomic classes of molluscs are less familiar: polyplacophorans are armoured slugs with metal teeth and millions of sensors embedded in their articulating shell armour; scaphopods are predators in a tubular shell with superelastic feeding tentacles; monoplacophorans are headless deep-sea limpets that were discovered alive only in 1957; finally, Solenogastres and Caudofoveata are two different types of worm-like molluscs that have no shells at all. Molluscs are the second largest animal phylum, in terms of species number they are only trumped by arthropods. But in terms of morphological diversity, or disparity, molluscs far outstrip arthropods and are the hands-down champions. If we could unpick the exact evolutionary relationships among the different groups of molluscs, it might help reveal the genomic traits that underpin this capacity for extreme morphological plasticity [1]. Two recent papers have provided important contributions to the pursuit of understanding molluscan disparity, touching on adaptations in both fossil and living members, with reports of an exceptionally preserved Ordovician stem chiton [2] and the first living records of a bizarre bivalve [3].

The eight crown group clades or taxonomic classes of molluscs are more or less unambiguously monophyletic, meaning each of them can be traced back to a last common ancestor. The splits among all of these clades occurred at some point relatively early in the Cambrian [4,5]. Textbooks and phylogenetic studies typically illustrate a set of eight archetypes that represent the forms of living molluscs. Species that deviate from those plans may often be interpreted as aberrations that are uninformative to the long-term narrative of molluscan morphological evolution. However, we increasingly come to understand that morphological weirdness is the

molluscan normal; this is a pattern evident from the diversity of living forms, and it is increasingly clear that morphological experimentation, including evolutionary dead ends and reversals, has been a constant feature of molluscs over more than 500 million years of their radiation.

What we understand about innovations in living lineages of molluscs indicates that they are particularly adept at fabricating mineralised armour. Gastropods have one shell, or two, or none: beyond the canonical one-shelled snails, there are sacoglossans (Juliidae) that were originally described as bivalves [6], and while slugs and pelagic gastropods have reduced or lost the shell, several groups also possess secondary armour of subdermal calcareous spicules [7]. Bivalves, classically two-shelled, similarly encompass a range of adaptive forms, including predators, periodically free-swimming animals and others that are permanently glued to the substratum, as well as worm-like ‘shipworm’ bivalves with bodies whose reduced shells rasp out their burrows in the substratum. The giant shipworm *Kuphus polythalamia* is the longest living bivalve (over 1.5 m long), and yet observations of the living animals were documented for the first time only recently [3]. These oddities illustrate the astonishing plasticity of the molluscan bodyplan, and they present a caution against generalities.

In some other groups of molluscs, the living forms look comparatively more alike though disparity seems to have waxed and waned over their long fossil record. Chitons (Polyplacophora) have an eight-part shell that has had a fairly consistent morphology for over 300 million years [8]. However, other fossil members attributed to Polyplacophora include seventeen-shelled monsters [9] and armoured worms [10]. Indeed, all of the known body fossils of paleoloricate ‘chitons’ from the Ordovician and Silurian had a worm-like body covered in spicular cuticle with no slug-like foot. These fossils are a key piece of evidence linking Polyplacophora and the two classes of worm-molluscs in the clade ‘Aculifera’. Early putative aculiferans fall into two dramatically different types, united only by comparison to crown group features: they generally either have seven or eight shells and no foot (e.g., *Phthipodoichiton* [10]), or a broad ventral foot and one or two solid shells, including the newly described taxon *Calvapilosa* [2]. This fossil mollusk had a single solid shell on a flat body otherwise covered in a scleritome. The slug-like body with a broad flat ventral foot is considered the primitive form among molluscs, and *Calvapilosa* can be compared with similar fossils, such as *Halkieria*, from much earlier in the Cambrian period. So it is interesting that this strange animal *Calvapilosa* in the Ordovician period extended

perhaps 50 million years or more beyond the likely primary separation of the most similar crown group classes (Polyplacophora, Solenogastres, Caudofoveata). This is diversity accumulated over time, approaching something like a normal level of disparity for a self-respecting molluscan clade.

Many molluscs were first described from the shell alone, and in the case of fossils the preserved remains may be disarticulated. Detailed anatomical observations of living animals, and exceptionally preserved fossils, are critically important to understanding the evolution of molluscs and indeed any organism. Exceptionally preserved fossils such as *Calvapilosa* preserve whole articulated scleritomes and other key anatomical features. In particular *Calvapilosa* shows an unambiguous radula [2], the rasping tongue ribbon that is a unifying feature of molluscs.

Dependency on shell characters, without context or anatomy, has precipitated confusion over the evolutionary relationships of many molluscs. Bivalves are unexpectedly enigmatic, being confused with some strange gastropods [6] and another fossil group called rostroconchs [11]. Shipworms are known mainly from the holes they bore into wood, and this is the plesiomorphic trait for that group of bivalves. The new study of the living giant shipworm *Kuphus polythalamia* showed that it evolved from a wood-feeding lifestyle, to a novel dependency on sulfide-feeding bacteria [3]. An evolutionary transition in the microbiome, associated with a new feeding mode, enabled such growth to enormous lengths. Several other species of the genus *Kuphus* are known from fossil tubes and achieve similarly impressive lengths. Gigantism was already found in Upper Cretaceous fossils attributed to the genus *Kuphus* that were probably the only molluscs ever to be confused with dinosaurs [12]. Insights to the anatomy of living animals guide our interpretation of fossils, and fossils reciprocally inform our understanding of the relationships among Recent taxa.

The question is, which morphological and ecological transitions have happened repeatedly, and which are potentially more constrained or more informative? A few parts of the molluscan evolutionary tree are well resolved. A close relationship of scaphopods, cephalopods and gastropods is supported by various approaches [13–15]. The clade Aculifera also has strong support [16,17]. Spicules and scale armour have evolved convergently in multiple gastropods [18] and also cephalopods [19]. Vermiform body plans have evolved over and over and over throughout Metazoa, so the position of the two aplacophoran classes should perhaps

be treated with some caution. The specific position of bivalves, and monoplacophorans, remains elusive.

We understand that the crown groups of the living mollusc classes were established by the end Cambrian. Fossils in the Ordovician should stratigraphically be interpreted as in the stem of an established clade; however, certain fossil groups may be the descendants of additional independent experiments in molluscan disparity (rostroconchs, for example). Molluscs are clearly capable of staggering and rapid evolutionary changes to their body plan morphology. This is a key trait that underpinned the early radiation of molluscs, and has continued unabated in most groups for more than 500 million years.

High resolution data on morphology remain vitally important in a research environment dominated by genomics as there is no other way to access to their early history. We must consider these early morphologies and mosaic taxa not only in relation to the textbook archetypes, but in relation to the demonstrated morphological capacity of molluscs. It is extraordinary that *Calvapilosa kroegeri*, which looks like some of the earliest Cambrian molluscs, was present in the Ordovician, after the crown group molluscs were already established. It is wonderful that *Kuphus polythalamia*, giant black worm-clams, are living in the Philippines, and only described in detail for the first time this year. We are only beginning to appreciate the evolutionary power of the molluscan body plan. This system remains an exciting frontier in evolutionary biology with many fossil and living discoveries still to be found.

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Figure 1. Some less familiar faces from the three largest groups of molluscs illustrate molluscan disparity. Left: the octopus *Grimptea* sp. (Photo: MBARI), centre: the bivalved gastropod *Berthelinia singaporensis* (Photo: Leena Wong), right: the 'watering pot' bivalve *Stirpulina ramosa* (Photo: Chong Chen).